THE STRUCTURE OF THE FLOWER OF NEWBERRYA

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Those plants, partly independent and partly saprophytic, which Engler and Prantl include in the family Pirolaceae (better spelled Pyrolaceae) are especially abundant in western North America. Pyrola, Chimaphila, and Monotropa are well known in many parts of the north temperate zone; in addition to these, the genera Sarcodes, Pterospora and Pleuricospora are well known to Californians. Representatives of the genus Newberrya, on the other hand, are rarities. Gray[1] described the genus from a plant collected by the Williamson expedition in the "Upper Des Chutes valley; September," 1855. The original description was erroneous in at least three respects. In the first place, the anthers, although recognizably represented in the plate, were comically misunderstood. Each anther was described as consisting of one fertile pollen sac and one sterile one. In consideration of this character, the plant was given the name Hemitomes, interpreted as "half-eunuch." Secondly, no disk or nectary was noticed. Thirdly, and with admitted uncertainty, the one-celled ovary was described as containing four bilamellate placentae. Torrey[2] presently corrected the description of the anther, and renamed the genus Newberrya, in honor of the botanist of the Williamson expedition. From Britton's[3] proposal to resurrect Hemitomes (he misspelled it Hemitones) we are apparently saved by the priority of Hemitomus L'Her. Newberrya seems first to have been collected in California by Rattan, who found it in two places in Humboldt County; one collection was identified by Gray[4] as the original Newberrya congesta, while the other was described as N. spicata. In the publication of these collections, Gray included description of a disk. When Small[5] treated the genus, he distinguished five species; three of these are known to this day, apparently, by single collections, and two of the three were known to Small only by description. The herbaria of Stanford University and of the University of California include a total of less than a dozen specimens.

When a fresh specimen which, with some doubt, I call Newberrya congesta, came to hand,[6] in June, 1932, I fixed parts of it

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[1] Rep. Expl. Pac. R. R. 6[2]: 80, pl. 12. 1857.

[2] Ann. Lyc. 8: 7. 1864. Non vidi.

[3] Bull. Torr. Bot. Club 20: 93. 1893. Gray's original plate is reprinted.

[4] Proc. Am. Acad. 15: 44. 1879.

[5] N. Am. Fl. 29: 17–18. 1914.

[6] The miserable scrap came to the herbarium of the University of California for identification. I have regretably lost all record of the name of collector and place of collection.

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in Bouin's fluid; and in due course sectioned the material and stained it, mostly with saffranin and light green. The material is scant. It includes no roots; nor are these present on any of the herbarium specimens which I have seen. One supposes a compact globular cluster, like those of Sarcodes, Pterospora, and Pleuricospora. Little of interest is discovered in the sections of a couple of scraps of stem. The vascular tissue forms a thin cylinder lying between the large pith and the cortex; it consists mostly of elongate, thin-walled cells, with scattered patches of lignified, mostly spiral elements, on the inner border. The cylinder is much interrupted by large gaps[7] where traces depart to the reduced vegetative leaves, the bracts, and the flowers. The compact terminal inflorescence is described by Jepson[8] as consisting of cymelets, in which the lateral flowers are generally bisepalous and otherwise tetramerous, while the terminal flowers have the parts in greater numbers. The flowers which I have seen conform to the description of the lateral flowers. They are all in approximately the same stage of development, showing mature pollen grains and ovules ready for fertilization. In dealing with a common plant, one would wait for more material; the rarity of Newberrya may justify the presentation of an incomplete description.

The flowers (fig. 1) stand in the axils of bracts as long as themselves. The pedicels are stout and very short. This is a useful diagnostic character; by long pedicels I was able to pick out several specimens of Monotropa (or Hypopitys) which had been confused with Newberrya in herbaria. The sepals in most flowers are two (four in the flower from which fig. 3 was drawn; the fourth is outside the field of vision). The sympetalous corolla is obconical, with four lobes, each of which may be described as shallowly four-lobed, or, in other terms, as emarginate and auriculate.

The interior of the corolla is in my material sparsely white-hairy. Jepson's description, agreeing with many herbarium specimens, makes the interior of the corolla densely white-hairy. This difference is probably of taxonomic import. The same white hairs are scattered over bracts, sepals, filaments, ovary and style, and even inside the style channel, but not on the stigmatic surface. They are most abundant toward the summits of the filaments and in a collar-like mass on the style just below the stigma. Each hair is an extension of an epidermal cell, not cut off by a cross wall at the base nor divided by walls elsewhere.

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[7] Where the departure of the vascular supply to each leaf produces a single breach in the vascular cylinder, the nodes are said to be unilacunar. *Cf.* Sinnott in Am. J. Bot. 1: 303–322. This is the state of affairs in Newberrya, as in all Ericales except Epacridaceae.

[8] Man. Fl. Pl. Calif. p. 739. 1925.

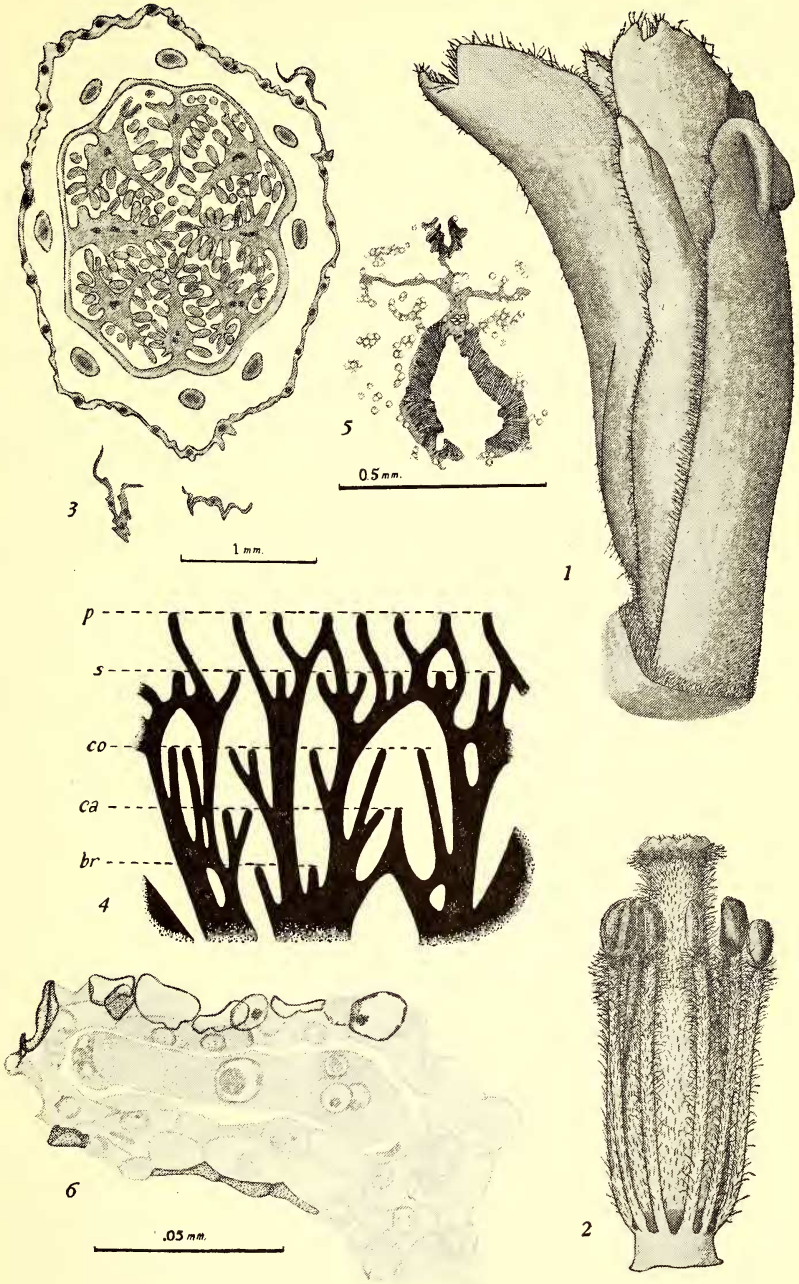

PLATE 1. NEWBERRYA CONGESTA TORR.

The hair tapers to an exceedingly minute rounded point. The walls are marked externally by very fine lengthwise ridges, sometimes slightly spirally twisted. The structure of the protoplast is not clear; masses of stainable material appear, alternating with unstained spaces.

Within the corolla a brief column bears the pistil and stamens. The stamens are usually eight (nine in the flower from which fig. 2 was drawn). All the anthers in my material have undergone dehiscence, but their structure is evident from cross sections (fig. 5): each includes four pollen sacs, of which the ventral pair are larger than the dorsal. There is no endothecium of ribbed cells as in most angiosperms. Excepting the outermost layer, the exothecium, the wall cells are almost completely absorbed (compare Samuelsson's[9] description of Loiseleuria and Leiophyllum, in which the structure of the anthers seems to be about the same). At first glance, the exothecium appears to consist of columnar, thick-walled cells; the fact, as nearly as I can make it out, is that they are originally nearly cubical, and that in contraction during dehiscence the walls are thrown into coarse wrinkles which give the columnar appearance. Dehiscence is through two lengthwise slits, which divide the wall into four valves; the valves swing outward till they are recurved, the edges of the two ventral valves meeting on one side, those of the dorsal valves meeting on the other. Gray originally mistook the space between the recurved ventral valves as a fertile pollen sac, and that between the dorsal valves as a sterile one. The pollen grains, as in Ericales in general, are binucleate; one nucleus is spherical, the other fusiform. The walls are smooth. As in other Monotropoideae, in distinction from Ericales in general, they are solitary, not in tetrads. These anthers call for comparison with those of Pterospora, Pleuricospora, Pityopus, and various species of Monotropa; but more data than we have must be assembled. Differences between the anthers of these various groups are known to exist; but resemblances of taxonomic significance will probably be discovered.

Oliver[10] described the nectaries of Sarcodes and of Monotropa glabra, and pointed out these structures as likely to be of taxonomic interest. In Newberrya, the disk is a belt around the base of the ovary, from which dark-colored knobs project downward between the bases of the filaments. These knobs are somewhat more prominent than the corresponding structures of Sarcodes, but are not curved together in pairs embracing the bases of alternate filaments, as in Monotropa glabra. The "biological significance" of the column bearing stamens, disk, and pistil may be that in raising these structures from the base of the corolla it leaves a space for the accumulation of nectar.

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[9] Svensk. Bot. Tijd. 7: 69–188. 1913.
[10] Ann. Bot. 4: 303–326. 1890.

The ovary is ovoid, the style brief, the capitate stigma divisible into eight lobes surrounding an eight-rayed orifice leading to the interior of the ovary. The ovary is one-celled. The interior is nearly filled by eight placentae lying in more or less the same radii of the flower as the stamens (the flower shown in fig. 2, having nine stamens, has nine placentae). In most previous publications, the placentae are described as bilamellate; in fact, in their best development, they are trilamellate and appear hastate in cross section. In the very bottom of the ovary, the lateral lamellae of adjacent placentae are coalescent, and the central lamellae fade out; the result is an appearance of eight lateral chambers surrounding a central one. In the upper part of the ovary, the lateral lamellae fade out, and the central ones continue upward as ridges in the style channel; they terminate as the lobes of the stigma. The whole ovary is of a structure of the ovaries found in other Ericales in the uppermost part, where the locules open into a central passage. It is evident that the eight placentae mark the boundaries of as many carpels. The stigmatic surfaces are of two kinds of cells, both full of dark-staining material. On the inner slope, toward the style channel, there are several layers of isodiametric cells; on the outer slope, toward the collar of hairs, there is on each lobe a single layer of closely packed columnar cells.

The placentae are covered with ovules. Each ovule (fig. 6) has an integument of two layers of cells, of which the outer layer stains differently from the inner, showing a marked affinity for saffranin. The embryo sac is of the normal type, having an egg apparatus of three cells, an endosperm mother cell containing (at this stage) one large nucleus, and three antipodal cells recognizable with difficulty. No trace of a nucellus is found at this stage. In all essentials, this is the usual ovule of Ericales and of sympetalous plants in general.

The vascular system of the flower is irregular. I puzzled out the relation of flower supply to bract supply only in one flower (fig. 4). One might expect the flower, standing in the axil of a bract, to be furnished with two traces, interpretable as running from the angles on the two sides of the bract trace where it swings out from the vascular cylinder of the stem. In the flower studied I found a third trace, formed by the bending inward of the middle part of the bract supply. The rest of the vascular system is described from three or four flowers. The several traces to the flower form an interrupted cylinder in the pedicel. Bundles supplying the sepals and corolla originate in no consistent fashion, and swing outward. Above the departure of these bundles, in the column, the vascular cylinder becomes more compact. Near the summit of the column the cylinder breaks up, essentially into sixteen bundles. Eight alternate bundles swing outward to supply the stamens. The other eight, being

recognizable as carpel traces, might be expected to fork trichotomously, each giving rise to a carpel dorsal bundle and two carpel ventrals. Actually, no carpel dorsals appear at this point; the bundles of the pistil supply, sometimes forking or anastomosing but usually merely swinging to the side, come to lie in the same radii of the flower as the stamens, and proceed upward in the placentae some distance inward from the ovary walls. They fade out in the upper part of the ovary. In the upper part of the ovary, and in the style, eight carpel dorsal bundles, each consisting of a few spiral tracheids, are found; they lie in the ovary wall, one of them between the radii of each two placentae. There is no connection between these bundles and the rest of the vascular system of the flower. The whole system gives an impression of erratic structure, related, presumably, to the saprophytic manner of life.

All authorities—Gray, Drude, Small, and Jepson—agree in placing Newberrya next to Pleuricospora. The possibility that Monotropa is quite as close a relative is suggested by a superficial yet striking character: in some species of Monotropa the pubescence of the pistil, including the collar below the stigma, resembles closely that of Newberrya. Drude[11] placed Newberrya and Monotropa in separate tribes; Monotropa is choripetalous and shows axile placentation. In classifying most groups, these characters would be accorded great weight, but among the saprophytic Ericales they appear to be unstable.

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Explanation of the Figures. Plate I

Fig. 1. Flower, × 5.

Fig. 2. Flower with perianth removed, × 5.

Fig. 3. Cross section of a flower, × 18. A fourth sepal, lying at a distance to the upper left, is omitted.

Fig. 4. Diagram of the course of bundles in a flower, based on serial sections of the flower represented in Fig. 1. The bundles are represented as seen from within the stem, and in the upper part as if the vascular cylinder were unrolled. *br,* bundles leading to the bract; *ca,* to the two sepals; *co,* to the corolla; *s,* to the stamens; *p,* to the pistil.

Fig. 5. Cross section of an anther, × 56.

Fig. 6. Longitudinal section of an ovule, × 490. The drawing is reconstructed from two adjacent sections, each 10 microns thick.

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[11] In Engler und Prantl Nat. Pflanzenfam. 4[1]: 3–11. 1891.